

Penetrantia clionoides, sp. nov. (Bryozoa), a Boring Bryozoan in Gastropod Shells From Guam

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Abstract. Gastropod shells from 15 sites around Guam contain specimens of a new species of boring bryozoan in the genus *Penetrantia*. This is the first boring bryozoan reported from the Mariana Islands and the first representative of the genus in the tropical Indo-West Pacific. The distinctive sculpturing on the upper surface of the operculum sets *Penetrantia clionoides* apart from other species in the genus. The new species is shown to be most similar to *Penetrantia operculata* from Hawaii. Scanning electron microscopy reveals previously unreported details of the ultrastructure of recent boring Bryozoa. Evidence of the inhibitory effects of crustose coralline algae on these borers is presented. The disputed systematic position of the boring bryozoans is discussed and the situation is shown to be complicated by the discovery here of an unusual form of aperture to the borehole, which displays both ctenostomate and cheilostomate characteristics.

Introduction

This report describes the first boring bryozoan in the genus *Penetrantia* from the tropical Indo-West Pacific. It is based on collections made around Guam as part of a larger study investigating the interactions among boring organisms (organisms that penetrate a calcareous substrate and live within it), gastropod shells, and crustose coralline algae. An unidentified borer occurred at all 15 study sites, boring mainly in the parietal region of the gastropod shells. Upon investigation, this organism was recognized as being a boring bryozoan.

The boring Bryozoa are an ethologically defined group of aberrant species that live within solid calcareous substrates in the marine environment (Pohowsky, 1978).

The substrates invaded are gastropods, pelecypods, brachiopods, and crinoids. D'Orbigny (1847) was the first to describe borings in mollusc shells made by bryozoans. It was not until 1938 that the anatomy of the zooids was presented (Marcus, 1938).

There are approximately 4,000 living species of ectoproct bryozoans with as many as 15,000 fossil species (Soule and Soule, 1969a). These organisms have diversified greatly and occur in the following forms: soft gelatinous colonies, fenestrate and squamous colonies, arborescent chitinous or calcareous colonies, single- or multi-layered crustose colonies, colonies boring into hard substrates and those burrowing into soft material. The four genera that burrow through soft material are (after Pohowsky, 1978); *Hypophorella expansa* Ehlers, 1876 in polychaete tubes (e.g., *Chaetopterus* and *Terebella*); *Watersiana paessleri* Calvet, 1912 in the tunic of the colonial ascidian, *Polyzoa gordiana*; *Harmeriella terrebrans* Borg, 1940, in the calcareous walls of cheilostome bryozoa; and *Bulbella abscondita* Braem, 1951, in rotting wood. Pohowsky (1978) reports that certain cheilostomes are known to produce shallow pits on encrusted shells (e.g., *Hippothoa divaricata* Lamouroux, 1821 and *Electra monostachys* (Busk), 1854). These latter burrowing and etching bryozoans are of interest in that they display characteristics intermediate between the true borers and the epifaunal bryozoans. Pohowsky (1978) reports that boring bryozoans penetrate exclusively by chemical means. There are, however, no data in the literature to support this statement. The four genera of Ctenostomata penetrating soft substrates are believed to employ mechanical techniques.

Because of the lack of investigation of boring bryozoans, little is known about their biology and ecology. Forty-eight species of borers (assigned to three genera) are known, but the anatomy of only sixteen has been described. The remaining species are known only by their tracings.

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Bryozoans have received little attention in the literature dealing with bioerosion. Indeed, many reviews of boring organisms fail to include any mention of the boring Bryozoa (*e.g.*, Warne, 1977). It is important to note that mollusc shells in general, and gastropod shells in particular, have been neglected in studies of bioerosion. This is the first systematic investigation of the boring organisms occurring in the three status categories of gastropod shells: living, hermited (*i.e.*, shells occupied by a hermit crab) and vacant shells. The need for such a study is obvious upon examination of the literature where, in the vast majority of publications dealing with borers in gastropod shells, the shell status is not mentioned. This leads to a loss of information regarding factors determining the longevity of a shell after death of the gastropod with consequences for conchicoles [a term proposed by Vermeij (1987) for organisms living within gastropod shells], encrusters, and for the ultimate composition of the fossil community.

In his major study of boring bryozoans, Pohowsky (1978) states that "their destructive activities appear to be far exceeded by those of boring sponges, thallophytes, and numerous other organisms." While this may be true for organisms that bore into coral, the results of this study show that it is not true for gastropods. This new species of bryozoan is the most common borer in gastropod shells on Guam, occupying 58% of all bored shells (Smyth, in prep.). In the case of bored living gastropods, 35.8% contained the bryozoan while 78.1% of bored hermited shells contained this species. In contrast, boring sponges occupied 9% of all bored shells. As this study indicates, it is clear that the importance of boring bryozoans to gastropod shells has been greatly underestimated.

Materials and Methods

During April–June 1982 and July–September 1984, living gastropods—as well as empty shells and those containing hermit crabs—were collected at 15 intertidal and shallow subtidal sites around Guam. Characteristics of the study sites will be detailed in a future paper. Areas were randomly chosen at each site and all shells within the area were collected.

After collection, a number of gastropods were maintained in the flow-through seawater system at the University of Guam Marine Laboratory for observation of the boring organisms. All shells were later preserved by oven-drying or by immersion in 4% buffered formalin or 70% ethanol. Wet-preserved shells were either immersed whole or fractured prior to preservation.

Upon return to the University of Maryland, the distribution and gross structure of the borings were determined by light microscopy. Chips were removed from whole shells using an ultra high speed precision air grinder (Dentsply Airotor, 300,000 rpm.) with Dentsply TRU-RUN (TM) carbide burs of 0.1 mm head diameter.

Selected shell pieces were chosen for detailed examination of the polypide and its borehole. For anatomical studies, formalin-fixed shell chips were decalcified in a 1% solution of 12 *N* hydrochloric acid in 70% ethanol. The HCl was added dropwise to the solution as required to maintain bubbling. The shell material dissolved entirely leaving the zooids interconnected by stolons. The zooids were then teased apart in 70% ethanol containing 5% glycerol on a microscope slide, stained with methylene blue and examined using light microscopy. Line drawings were prepared from camera lucida projections. Tentacle counts were obtained by making squashes of 67 zooids. In eight cases, a clear spread was achieved, revealing the number of tentacles in the lophophore.

Chips from 21 shells were prepared for scanning electron microscopy (SEM) to examine the borehole and its associated tissues. Most of the selected chips were used directly upon removal from alcohol, though a small number of those used had been in the decalcifying mixture for various periods of time. The chips were dehydrated with a graded series of ethanols, cleaned ultrasonically and dried in a critical point dryer (Denton Vacuum, Inc., DCP-1). The chips were glued onto glass cover slips with a dilute water-soluble glue (trade name, "Elmer's Glue-All", Borden Inc.). The coverslip was then attached to a standard aluminum stub by carbon paint. The specimens were later sputter-coated under vacuum, first with a thin layer of carbon and then with gold palladium. They were viewed with a Cambridge Stereoscan Electron Microscope, Model 100. Stereo pairs were taken with a 7° tilt of the specimen. Magnifications of all SEM photomicrographs, and therefore measurements, have a $\pm 5\%$ margin of error.

Individual opercula were isolated by placing bored shell chips in a solution of commercial grade laundry bleach (5% NaOCl) overnight. This freed the opercula. Eleven of these opercula then underwent numerous washings in distilled water, were air-dried, manipulated with fine watchmaker's forceps, and glued onto glass coverslips. They were then prepared for SEM in the manner described above. X-ray analysis of opercula was carried out using a TN-2000 Multi-Channel Analyzer connected to a Cambridge Stereoscan Model 250 Scanning Electron Microscope operating in the Time Scan Mode. The X-rays produced were representative of the elemental composition of the sample at the point being scanned. The resulting X-ray spectrum, showing peaks indicative of concentrations of various elements, is presented as a dot distribution map.

Systematic Account

PHYLUM Bryozoa Ehrenberg, 1831
SUBPHYLUM Ectoprocta Nitsche, 1869
CLASS Gymnolaemata Allman, 1856

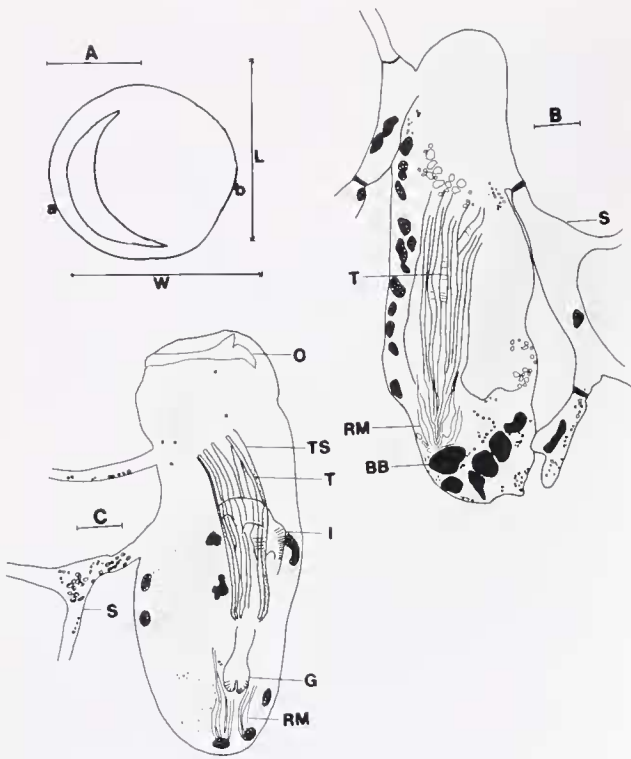


Figure 1. *Penetrantia clionoides* sp. nov. (A) Outline of operculum, indicating terminology used in text. Key: L = length of operculum, W = width of operculum. (B), (C) Anatomy of mature autozooids. Key: BB = brown body, G = gizzard, I = intestine, O = operculum, RM = retractor muscle, S = stolon, T = tentacle, TS = tentacle sheath. Scale bar = 50 μ m.

ORDER Cheilostomata Busk, 1852
SUBORDER Anasca Levinsen, 1909
FAMILY Penetrantiidae Silen, 1946
GENUS *Penetrantia* Silen, 1946

Penetrantia clionoides sp. nov. (Fig. 1)

Diagnosis: Boring colonial ectoproct bryozoans with autozooids and gonozooids connected by stolons. Autozooids elongated, cylindrical; aperture closed by operculum; operculum elliptical in outline with a distinctive crescent-shaped toothed area on upper surface; tentacle number 12. Gonozooid half the length of autozooid.

Type Locality: At 0–0.5 m depth on the algal ridge and in ridge pools, Pago Bay, Guam.

Hosts: Gastropods as indicated in Appendix 1.

Type Material: Holotype (USNM 417305) and two paratypes (USNM 417306 and 417307) deposited on slides in the National Museum of Natural History, Smithsonian Institution, Washington DC.

Etymology: -oides = “resembling,” derived from Gr. eidos = likeness.

Cliona-like; for the similarity of the boreholes, in surface view, to those of the boring sponge, *Cliona* sp.

Description: Each autozooid possesses a polypide bearing 12 tentacles and a typical U-shaped digestive tract.

The gizzard opens into the stomach. The muscular system consists of retractor muscles, apertural muscles and parietal muscle fibers (Fig. 1B, C).

The aperture (Fig. 2A–D) is closed by an operculum, which is diagnostic. The operculum is approximately elliptical in outline with a smooth circumference and a width to length ratio of 1:1 (Fig. 1A, 3A–D).

The upper surface of the operculum consists of a shallow conical mound with a crescent-shaped area to one side of the apex of the cone (Fig. 3A). The toothed crescent (Fig. 3B), consisting of overlapping chips of calcium carbonate, lies at an angle of $30^\circ (\pm 5^\circ)$ to the plane of the operculum. At the anterior end, these chips are grouped into larger accumulations forming teeth (Fig. 3B), the number of which varies between 14 and 16.

The undersurface of the operculum is a smooth disc with two diametrically opposed protrusions extending approximately perpendicular to the plane of the disc at its perimeter, half way between the anterior and posterior surfaces (Fig. 3D). An arced ridge connects the two protrusions and a thickened area lies on the undersurface of the lip. In one specimen, two slits were seen on the undersurface of the operculum, running parallel to and adjacent to each edge, and appearing to be scars of the opercular retractor muscles.

The average dimensions of the operculum (terminology as in Fig. 1A) are: width (W), 95.47 μ m, n = 20; length (L), 90.33 μ m, n = 8; depth at a, 12.53 μ m, n = 4; depth at b, 4.52 μ m, n = 3; maximum depth 46.35 μ m, n = 3. Values for opercular length vary from 81.8 μ m to

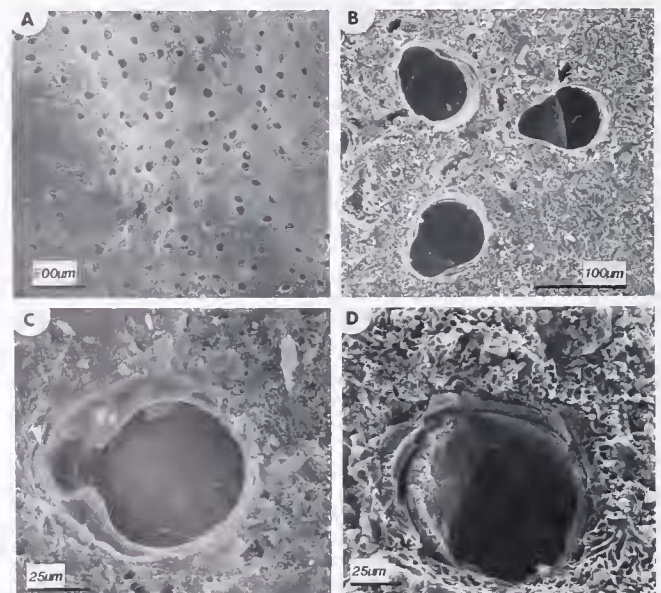


Figure 2. Borehole apertures of *Penetrantia clionoides* sp. nov. (A) Shell surface showing characteristic shape of borehole apertures. (B) Typical borehole apertures with one operculum open. (C) Rare key-hole-shaped borehole aperture showing ascophoran cheilostome-like anter and narrower poster (arrow). (D) Open operculum.

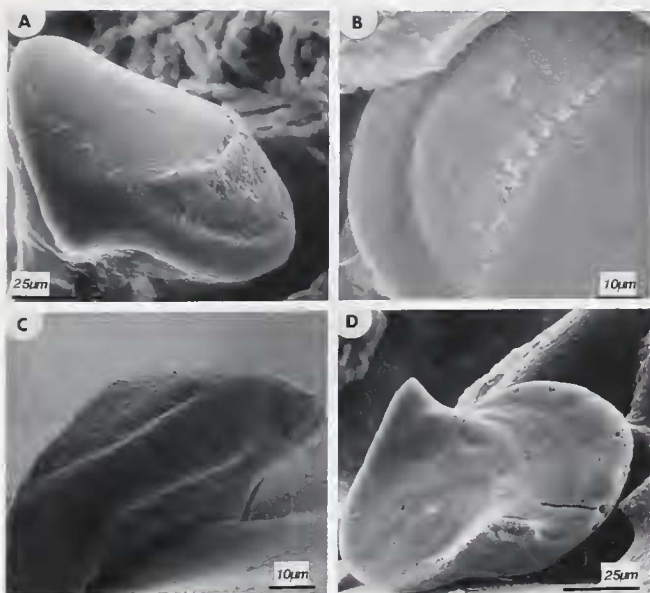


Figure 3. Loosened opercula of *Penetrantia clionoides* sp. nov. (A) Dorsal view of operculum. (B) Detail of toothed ridge on anterior surface of operculum. (C) Lip on anterior end of operculum. (D) Ventral view of operculum showing the two diametrically opposed protrusions.

97.1 μm and for width vary from 68.8 μm to 108.9 μm . The operculum is thinnest at its hind edge and thickest at the rear of the crescent.

Examination of the dot distribution maps indicates that the opercula are composed mainly of calcium car-

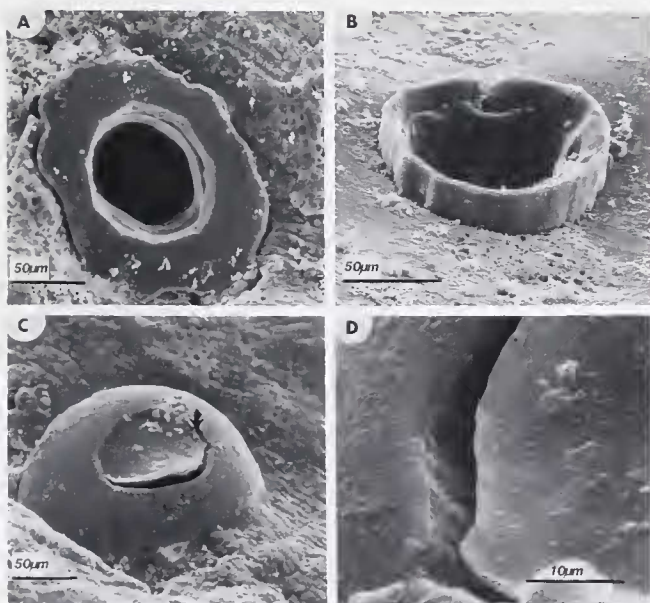


Figure 4. Unusual borehole apertures of *Penetrantia clionoides* sp. nov. (A) Calcareous irregular margin around aperture. (B) Raised margin. (C) Plug in calcareous margin. (D) Higher magnification of 'C' (ar-row).

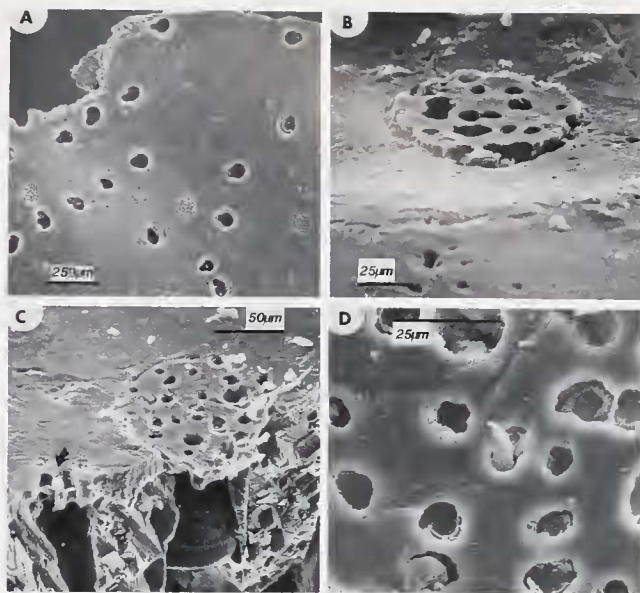


Figure 5. Borehole apertures and sieves of *Penetrantia clionoides* sp. nov. (A) Surface view of borehole apertures, sieves and individual holes. (B) Sieve. (C) Sieve over fully formed polypide complete with operculum. Note early stage of bryozoan borehole (arrow). (D) Detail of sieve in 'C'.

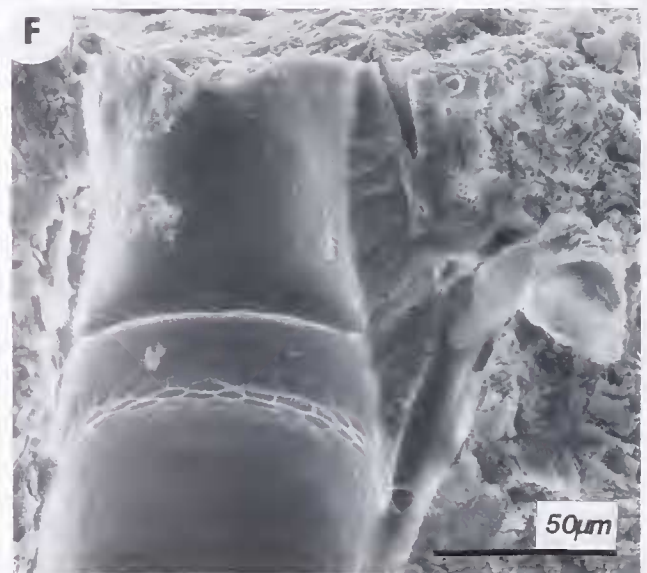
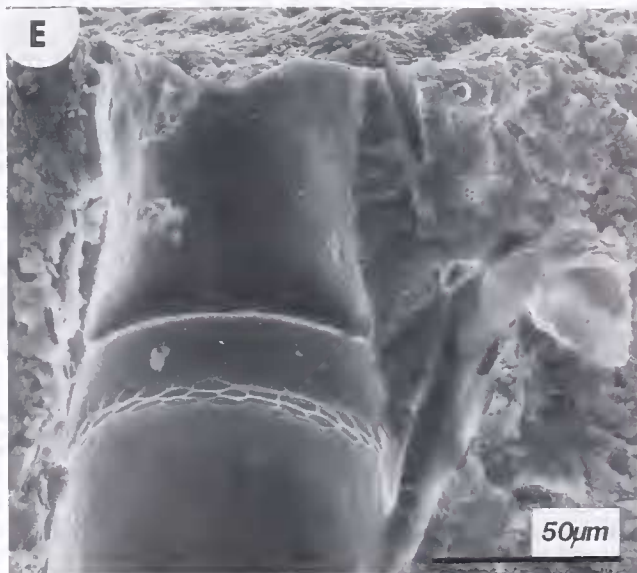
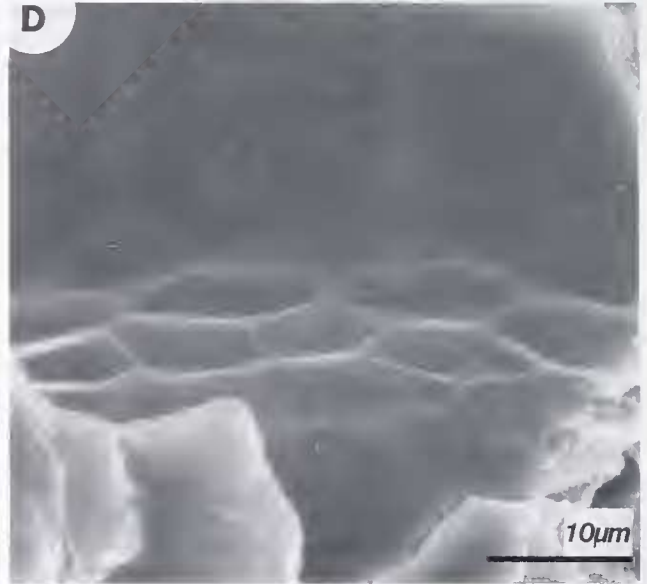
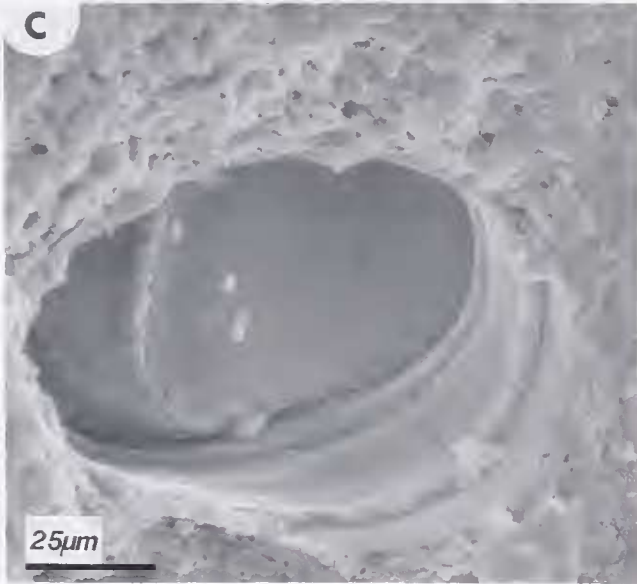
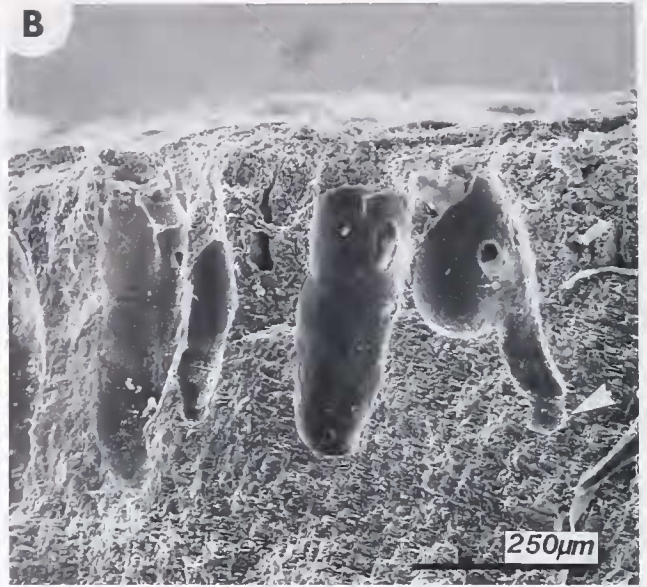
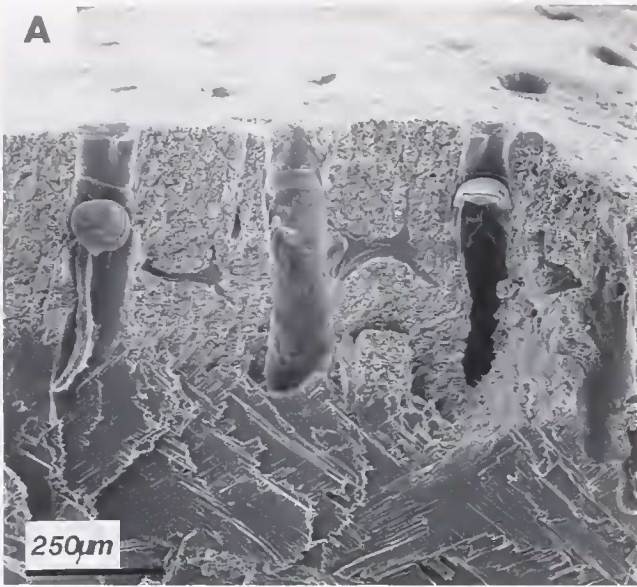
bonate with traces of sodium, zinc, magnesium, and aluminum.

Burrow apertures occur randomly on the outer surface of the mollusc shell (Fig. 2A). Statistical analyses (G-test of goodness of fit) show that even in colonies in the early stages of development, the pattern is random.

The shape of the aperture of the borehole is variable, from approximately circular to keyhole-shaped (Fig. 2A–D). In the latter case, the crescent lies in the narrow region of the aperture (Fig. 2B). These apertures are of the typical ascophoran cheilostome form with an anter and poster (Fig. 2C).

On rare occasions, the lining of a borehole is raised above the surrounding substrate (Fig. 4B). In only eight cases, an irregularly shaped calcareous margin was seen around a borehole aperture (Fig. 4A). Three of these margins are plugged in the center (Fig. 4C, 4D), not with an operculum but with a structure that appears to be about to detach (Fig. 4C).

Shells bored by *P. clionoides* are often seen with a number of white, circular areas (henceforth called "sieves") on the shell surface. These are perforated and of equivalent size to that of the borehole apertures (Fig. 5A–D). Interspersed among these sieves are accumulations of small holes, each hole equivalent in size to the individual holes making up a sieve (Fig. 5A). By fracturing one of the sieves, perpendicular to the shell surface, it was revealed that the sieve lies above a fully formed polypide complete with operculum (Fig. 5C). A long, narrow borehole next to this may represent the early



stage of a bryozoan borehole (Fig. 5C, arrow). The data indicate that sieves occur where more than two stolons meet.

The borehole of the autozoid lies perpendicular to the shell surface and is cylindrical with a bluntly rounded proximal end (Fig. 6A, B). The average dimensions are: depth of borehole, 410.24 μm , $n = 36$; width of borehole, 103.49 μm , $n = 25$.

The inner surface of the borehole is featureless except for a narrow zone beginning, on average, $\frac{1}{6}$ of the way along its length from the distal end. At its most distal end this zone consists of a thin ledge lying 72.2 μm , $n = 6$, below the shell surface (Fig. 6E, F). This ledge is, on average, 28.2 μm thick, $n = 6$. The upper surface of the operculum abuts against the undersurface of this ledge (Fig. 6C). The proximal end of this zone has a mesh-like appearance (Fig. 6D). This meshed area sometimes extends down entirely from the ledge. A nodule protrudes as part of the ledge at the proximal end of this meshed area and functions in articulation with the operculum (Fig. 7B). The operculum is closed by a pair of occlusor muscles, one arising on each side of the zoid and converging to a tendon which inserts on the operculum. The occlusor muscle inserts behind the protrusions (Fig. 7B).

The operculum is attached to the zooecium along its entire perimeter. At the posterior surface, a muscular connection links the operculum to the zooecium (Fig. 7A, 7F). This tissue is exposed when the operculum is open.

When the operculum is open, its posterior end protrudes from the borehole with the anterior end positioned out of view inside the borehole (Fig. 2D). As a result of examination of opercula found in the open position it appears that the operculum pivots on its two protrusions. These appear to articulate with the nodules seen on the wall of the borehole (Fig. 7B–E).

Occasionally, boreholes occur in such proximity to each other that only a thin area of shell remains between them. Up to 60% of the boreholes in a shell may be devoid of the polypide.

On average, the borehole of the gonozoid (Fig. 8B) is half the depth of the autozoid. Gonozoids include a bulbous embryo chamber which appears to emanate on either the right or the left side of the gonozoid, though it is possible that some of the samples observed are complementary fracture faces.

Boreholes differing from the usual cylindrical type are occasionally seen. These have an additional chamber on the proximal end that may represent a growing edge.

There are also shorter and wider boreholes, in the shape of gonozoids, but with the extension on the proximal end. These appear to be heterozoids (Fig. 8A).

Stolons emanate from zooids by a lateral branch at the distal end. Stolonal tracings are not seen on the shell surface until after soaking in acidic solution (Fig. 8C, 8D). In the intact shell, then, the only indication of the presence of *P. clionoides* is the occurrence of borehole apertures on the shell surface. On average, the diameter of a stolon is 9.8 μm , $n = 6$.

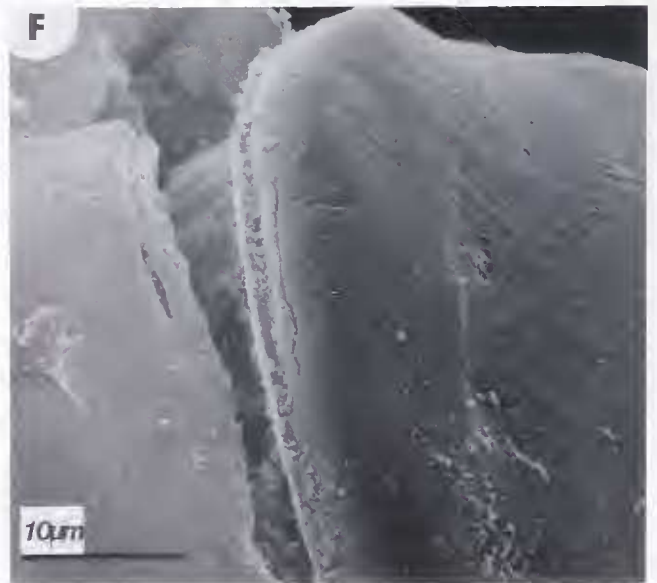
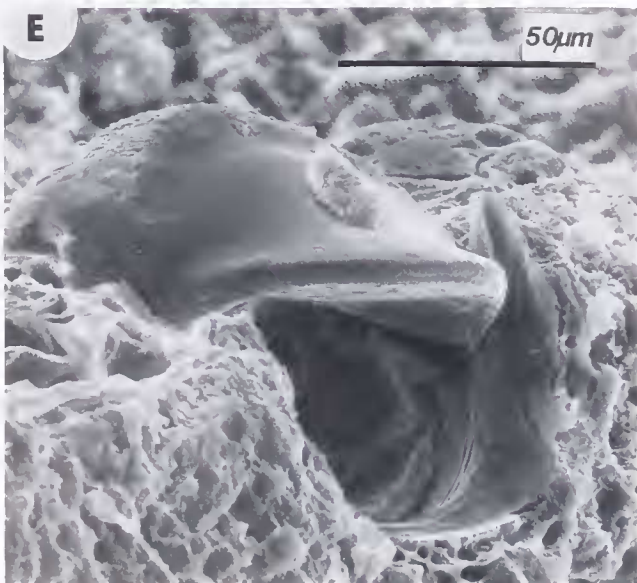
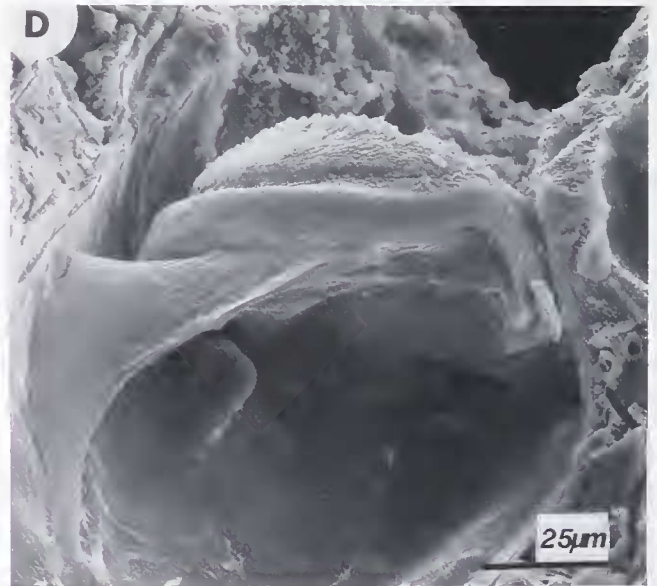
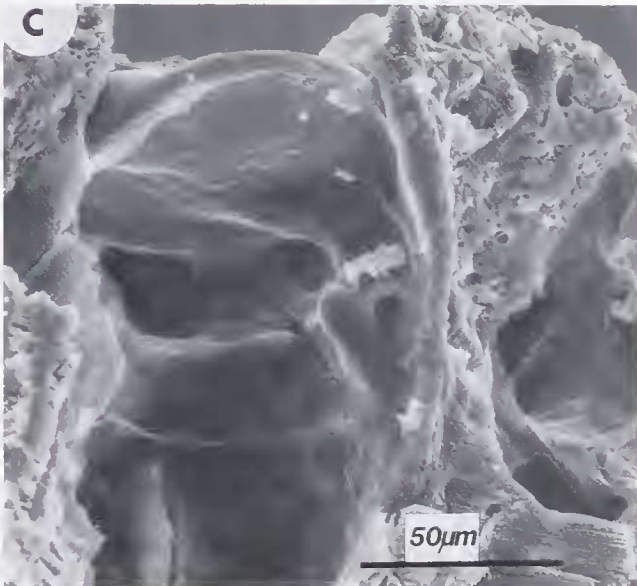
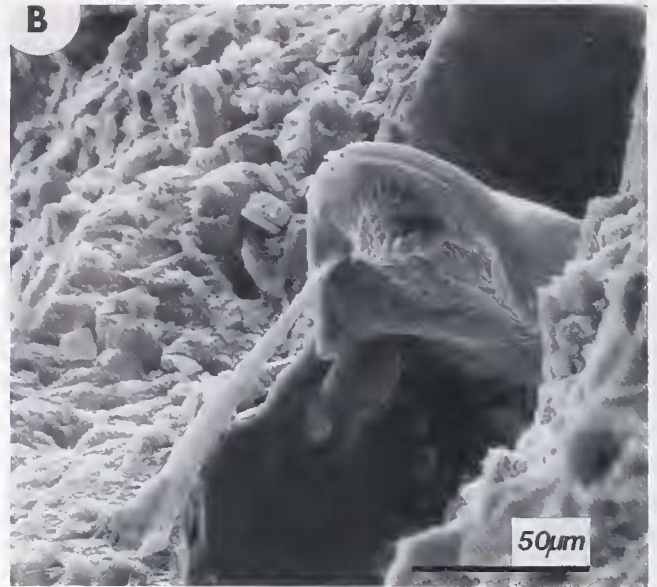
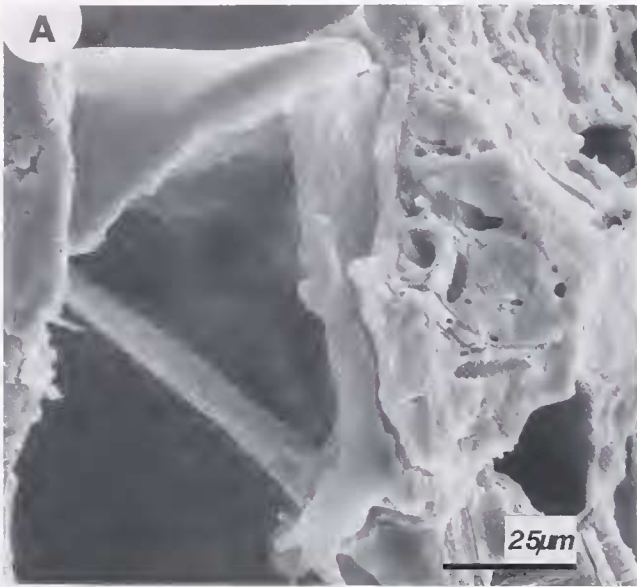
Penetrantia clionoides may occur in association with one or more of the other boring organisms (acrothoracican barnacles, clionid sponges, polydorid polychaetes, and the boring foraminiferan, *Cymbaloporella tabellaeformis*) occurring in gastropod shells at these study sites (Smyth, in prep.).

The susceptibility of *P. clionoides* to suffocation by overgrowth is indicated by its inability to maintain openings through coralline algae. A case of confinement, with corallines overgrowing a borehole aperture and trapping the bryozoan, is seen in Figure 9A. The other boring organisms in this study are capable of maintaining openings through corallines. Detailed examination of the parietal wall area of the shell (area on right side of shell aperture) has resulted in the discovery of a number of bryozoan boreholes enveloped by recently deposited shell material. As the shell grows, the boreholes become absorbed into the parietal wall area (Fig. 9B). In a living specimen of *Drupa morum* a bryozoan aperture, on the upper right side of the shell aperture, was in the process of being overgrown by the smooth shell of the outer lip (Fig. 9B). Clearly, this is a transient stage, but enveloped boreholes are often seen along the margin of the parietal wall and the inner lip (that is, where the smooth shell of the parietal wall meets the rough, encrusted shell of the inner lip area). Using light microscopy, these borehole apertures can be seen as white, translucent spots in the shell material.

Observations of broken opercula indicate that the operculum is hollow (Fig. 9C). This hollow region is lined with crystals resembling those of the crescent in structure. A fracture in the protrusion on the side of an operculum shows that these flanges are not hollow.

A number of bryozoan boreholes, devoid of polypide and operculum, were occupied by unusual crustacean-like organisms as yet unidentified (Fig. 9D). These bear some resemblance to harpacticoid copepods (pers. comm.; R. Cressey, Curator of Crustacea, Smithsonian Institution).

Figure 6. Boreholes of *Penetrantia clionoides* sp. nov. (A) Three boreholes in section. (B) Detail of 'A' showing ledges in borehole and stolonal tracings. (C) Upper surface of operculum abutting against undersurface of upper ledge. (D) Meshed area at top of borehole. (E), (F) Stereo pair of meshed area at top of borehole taken at 7° tilt.



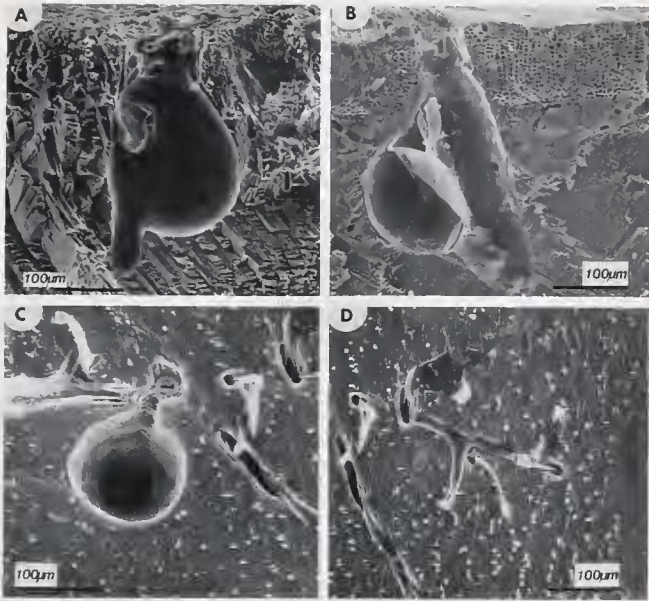


Figure 8. Stolons and unusual boreholes of *Penetrantia clionoides* sp. nov. (A) Probable heterozooid borehole. (B) Gonozooid with bulbous embryo chamber on left and operculum. (C) Stolons and section through boreholes in acid-treated shell. (D) Stolons on surface of acid-treated shell.

As a hermit shell is carried by its occupant, those corallines on the left of the aperture become worn off as a consequence of abrasion with the substrate. This results in a bare patch extending ventrally along the periphery of the aperture, which is invaded by the bryozoan.

Remarks

Penetrantia clionoides can be distinguished from all other members of the genus by its distinctive operculum. The species to which *P. clionoides* is most similar is *P. operculata* described from Haena Bay, Kauai, Hawaii (Soule and Soule, 1969b). The operculum of *P. operculata* is described as "a massive knobbed operculum" though no dimensions are presented. This operculum differs from that of *P. clionoides* in the absence of the crescent and of the other distinctive features of the operculum of *P. clionoides*. The differences between the latter operculum and that of *P. operculata* are major. Pouyet and David (1979), working with the genus *Steginoporella*, point out that opercular differences provide justification for separation into distinct species.

Discussion

Presently, it is generally accepted that the genus *Penetrantia* belongs in the suborder Anasca of the Cheilostomata. An operculum is characteristic of cheilostome bryozoans (Ryland, 1970). Nevertheless, scant attention appears to have been paid to its shape, composition, and method of articulation. This report presents the first detailed study of a recent bryozoan operculum including the first SEM micrographs of such an operculum. The operculum of *P. clionoides* is shown to be calcareous. Totally or partially calcareous opercula are apparently very rare in recent Cheilostomata (Voigt, 1974). There appear to be a number of similarities with the operculum of *Inversaria tubiporacea* from the Dutch Maastrichtian Chalk-tuff. Voigt (1974) points out that this operculum deviates in its shape to such a large extent from the opercula of recent Cheilostomata that, in isolation, it would never be taken for a bryozoan operculum but for a problematic microfossil. The conical outgrowth on the upper surface of the operculum of *P. clionoides* and the protrusions on the undersurface are, to a degree, comparable to those on *I. tubiporacea*.

There is no agreement as to the systematic position of boring bryozoans. Soule and Soule (1969a) removed the Penetrantiidae to the Cheilostomata but the most recent major study of the group (Pohowsky, 1978) regards all boring bryozoans as members of the order Ctenostomata, though with slight reservations regarding the Penetrantiidae. Representatives of the order Cheilostomata possess one or more of the following features: an ovicell, operculum, and calcified body wall. Pohowsky (1978) concedes that all three of the cheilostomatous characters are present in *Penetrantia densa* Silen, but argues that this is an example of convergence with the cheilostomes. Voigt (in Voigt and Soule, 1973) believes that a ctenostomatous relationship for *Penetrantia* cannot be totally excluded. In summary, the literature suggests that either the boring Bryozoa are a small obscure group specialized for the boring mode of existence (as in Pohowsky, 1978) or that boring constitutes an important ecological niche for bryozoans (as in Soule and Soule, 1969a). It is clear that this taxonomic issue cannot be resolved until the anatomy of the various borers is investigated in detail. For the moment, I accept the classification presented by Soule and Soule (1969a), though with some reservations because it is clear that characters have arisen independently in more than one lineage of bryozoans.

Figure 7. Articulation of opercula of *Penetrantia clionoides* sp. nov. (A) Operculum *in situ* showing opening and closing mechanism. (B) Posterior view of operculum showing tendon inserting on operculum and articulation with nodule. (C) Posterior view of operculum. (D) Operculum showing nodule and part of zooecial attachment. (E) Operculum in open position with posterior end protruding. (F) Attachment of operculum to zooecium at perimeter.

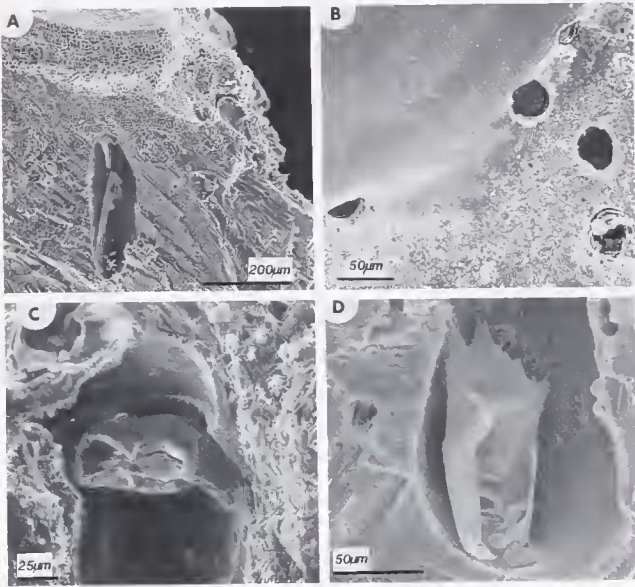


Figure 9. Overgrowth of *Penetrantia clionoides* sp. nov. (A) Borehole overgrown by crustose coralline algae. (B) Boreholes enveloped by recently deposited shell material in parietal wall area of shell. (C) Broken operculum indicating its hollow nature. (D) Empty borehole occupied by unidentified crustacean nestler.

Further investigation may show that because *P. clionoides* has features that overlap so much between ctenostomate and cheilostomate characters, a major reclassification is necessary. It seems that the generally accepted classification must eventually be abandoned. This study has introduced some data that make the issue of the systematic position of these boring bryozoans more confused. The presence of the rare keyhole-shaped burrow apertures is such a factor. These apertures are of the typical ascophoran cheilostome form with an anter and poster in the operculum. In the ascophoran aperture, the anterior part (anter) covers the passage for the polypide and the posterior part (poster) simultaneously covers the inlet to the compensatrix (compensation sac). Water enters the compensation sac to equalize space occupied by the polypide. The presence or absence of a compensation sac has been important for determining the appropriate suborder (*Anasca*, *Ascophora*). *Penetrantia clionoides* has some characteristics of both orders and suggests the inappropriateness of the criteria on which these orders are based. This problem has been addressed in the past. In fact, Silen (1942) combined the ctenostomes with the cheilostomes as the Cheilostenostomata. Ryland (1970) suggested that the division into the two suborders, *Anasca* and *Ascophora*, is invalid. He recognized four major divisions in the Cheilostomata. As Bassler (1953) indicated, "a classification of the Bryozoa that finally may be judged acceptable is impossible at present, because probably each family should be characterized essentially by

the larval form of its constituents; unfortunately, this is known at present for comparatively few families."

The opercula are remarkably non-encrusted relative to other structures I have examined on the surface of these shells. The movement of the operculum itself or some behavioral or chemical feature of the organism may be responsible for this.

The function of the plug in the calcareous margins around the burrow apertures has not yet been determined. I suggest that such a structure might be a closure device sealing off the polypide as it undergoes regeneration. However, the low incidence of these is puzzling in light of the purported high frequency of regeneration in boring bryozoans.

Budding pattern is defined by Pohowsky (1978) as "the geometric and sequential relationship existing among the stolons and zooids in a colony." It is generally assumed that boring bryozoans have a characteristic non-random budding pattern that is distinctive and easily recognized on the shell surface. It became evident during this study that such an assumption can be misleading. I witnessed situations where the presence of boring bryozoans is discounted because the budding pattern displayed by the borer does not conform with that previously published for bryozoans.

As a consequence of their appearance and the absence of the expected non-random "characteristic" budding pattern, the boreholes were initially assumed to be young clionid borings. However, fracturing the boreholes revealed the presence of opercula plugging the borehole apertures. This eventually led to the determination of the bryozoan nature of the burrows. Boekschoten (1966) reported a similar confusion in surface view.

The boring habit is generally assumed to have arisen as a means of refuge; organisms that bore are less vulnerable to predation. While *P. clionoides* is protected by being recessed in the shell material and by the presence of the operculum, there remains a degree of vulnerability. The main sources of mortality for these organisms are overgrowth/suffocation and predation. In this respect, it is interesting to note that the zooids of boring bryozoans are much less closely packed than are zooids of other bryozoans. The adaptive value of this is that if encrustation and overgrowth occur, there is a greater likelihood that part of the colony will survive to reproduce. Of the variety of boring organisms occurring in gastropods at these study sites, only the boring Bryozoa appear to be susceptible to interference by the gastropod. The tendency of these organisms to bore in the inner lip area leaves them in a transient situation where, unless the gastropod is dead or has reached its terminal growth stage, they will eventually be absorbed into the shell material as the gastropod grows. Hermit shells provide a more stable environment in terms of lack of interference from the shell-dweller. However, other factors come into

play—such as the greater likelihood of being overgrown by encrusters—in hermit shells. Their susceptibility to suffocation by overgrowth is indicated by the discovery of their inability to maintain openings through coralline algae. Thus it is clear that a calcium carbonate substrate is not always a source of protection for organisms living within it. Abrasion, borings, fracture, and encrustation are among the problems encountered.

There is no evidence of the existence of predators on Guam that gain access by drilling through the operculum. Having observed thousands of opercula, not one drillhole was seen. Taylor (1982) records pycnogonids and nudibranchs as major predators of Bryozoa, but no evidence of the effects of these specialized predators was seen in this large collection. Cairns (1982) saw circular boreholes in a calcareous stylasterine operculum from the Antarctic, but he argues against a molluscan predator without offering any alternative suggestions. The fact that the operculum is recessed may reduce the likelihood of predation by drilling. Presumably, many predators are unable to cope with the operculum. Hayward and Ryland (1969) report that some dorids push the operculum aside or into the zooid, and Ryland (1976) shows that it may be torn out. Pycnogonid predators allow a polypide to emerge and then rapidly dart the proboscis through the orifice and devour the contents (Wyer and King, 1973). Apparently, this has been observed only for the suborder Anasca. The zooids are attacked singly and are presumed to regenerate polypides later.

Vermeij (1978) documented a Mesozoic revolution in marine faunae which he attributed largely to the evolution of new predators. Larwood and Taylor (1981) show that evidence from the Bryozoa provides support for Vermeij's hypothesis because several features of Mesozoic bryozoan evolution can be interpreted as responses to increasing levels of predation. An example is the evolution of operculate autozooids and mandibulate polymorphs in two independent groups (cheilostomes and meliceritid cyclostomes). These authors point out that predation pressure may have been an important selective force operating on bryozoans during the Mesozoic, although direct evidence of paleopredation is limited.

There is no evidence that boring bryozoans are parasitic on mollusc tissue (Pohowsky, 1978). Pohowsky further shows that their occurrence in empty shells indicates their non-parasitic nature. In the case of the gastropod shells in this study it is clear that, as a consequence of the dimensions of the borings, they do not penetrate sufficiently deep to come into contact with gastropod tissue.

As a consequence of the small size of these zooids, the shell weakening effects would not be expected to be great. However, the tendency to concentrate in high density on the left side of the aperture must make this area more vulnerable to peeling or crushing predators.

Vacant bryozoan boreholes provide a space resource

for other organisms in the habitat. The existence of these nestlers emphasizes the complexity of issues associated with boring: not only the issues of bioerosion and consequent effects upon the bored substrate but also the additional space resource provided for other organisms.

The concentration of bryozoan boreholes in areas on hermit shells where the coralline algae are worn away is of great significance. This negative association between boring bryozoans and crustose coralline algae was discovered during an investigation of interference, by corallines, with the settlement of larvae of boring organisms on gastropod shells (Smyth, in prep.). Most shells in this collection come from areas with high surf, where crustose coralline cover is intense. Hermit shells are more heavily encrusted with corallines than are living gastropods, in part because of their greater age. If boring Bryozoa are seen on a hermit shell, they are seen only in the bare areas on the left side of the aperture. Examination of surrounding areas of the shell, under the coralline, rarely reveals evidence of the Bryozoa having been overgrown by the corallines. When bryozoan borings are seen in living gastropods it is, again, only in bare patches. In the latter case, the patches are scattered over the shell surface.

Future work includes examination of the larvae and observations of their settlement behavior, field experiments to determine the magnitude of shell weakening and vulnerability to peeling or crushing predators, and further studies to clarify the systematic position of the group.

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Appendix 1

Species of gastropod collected at 15 study sites around Guam

Gastropod	Presence/Absence of <i>Penetrantia clionoides</i>	Gastropod	Presence/Absence of <i>Penetrantia clionoides</i>
<i>Bursa bufonia</i> (Gmelin, 1791)	+	<i>Latirus barclayii</i> (Reeve, 1847)	+
<i>Bursa cruentata</i> (Sowerby, 1835)	+	<i>Morula granulata</i> (Duclos, 1832)	+
<i>Bursa</i> sp.	+	<i>Morula</i> sp.	+
<i>Bursa verrucosa</i> (Sowerby, 1825)	+	<i>Morula uva</i> (Roeding, 1798)	+
<i>Cantharus</i> sp.	+	<i>Nassa sarta</i> (Bruguière, 1789)	+
<i>Cantharus undosus</i> (Linnaeus, 1758)	+	<i>Patella flexuosa</i> Quoy & Gaimard, 1834	–
<i>Casmaria ponderosa</i> (Gmelin, 1791)	+	<i>Sabia conica</i> (Schumacher, 1817)	+
<i>Cellana radiata orientalis</i> (Pilsbry, 1891)	–	<i>Strigatella pauperkulata</i> (Linnaeus, 1758)	+
<i>Cerithium nodulosum</i> Bruguière, 1792	+	<i>Strombus luhuanus</i> Linnaeus, 1758	–
<i>Cerithium</i> sp.	+	<i>Strombus mutabilis</i> Swainson, 1821	–
<i>Chicoreus brunneus</i> (Link, 1807)	+	<i>Strombus</i> sp.	+
<i>Chicoreus</i> sp.	+	<i>Tectus pyramis</i> (Born, 1778)	+
<i>Conus</i> sp.	+	<i>Trochus maculatus</i> Linnaeus, 1758	+
<i>Coralliophila violacea</i> (Kiener, 1836A)	+	<i>Trochus niloticus</i> Linnaeus, 1767	+
Cowrie	+	<i>Trochus ochroleucus</i> Gmelin, 1791	+
<i>Cymatium nicobaricum</i> (Roeding, 1798)	+	<i>Trochus</i> sp.	+
<i>Drupa arachnoides</i> Lamarck, 1816	+	<i>Thais armigera</i> Link, 1807	+
<i>Drupa clathrata</i> Lamarck, 1816	+	<i>Thais intermedia</i> Kiener, 1836	+
<i>Drupa morum</i> Roeding, 1798	+	<i>Thais</i> sp.	+
<i>Drupa ricina</i> (Linnaeus, 1758)	+	<i>Thais tuberosa</i> Roeding, 1798	+
<i>Drupa rubisidaeus</i> Roeding, 1798	+	<i>Turbo setosus</i> Gmelin, 1791	+
<i>Drupa</i> sp.	+	<i>Vasum ceramicum</i> (Linnaeus, 1758)	+
<i>Drupella elata</i> (Blainville, 1832)	–	<i>Vasum</i> sp.	+
<i>Lambis</i> sp.	–	<i>Vasum turbinellus</i> (Linnaeus, 1758)	+

Presence or absence of *Penetrantia clionoides* in that particular gastropod species indicated by “+” or “–”, respectively. Rare species (sample size < 10 shells) excluded.